

## STRUCTURE OF THE ACOUSTIC SIGNALS OF *CRINIA GLAUERTI* (ANURA: MYOBATRACHIDAE) FROM SOUTH-WESTERN AUSTRALIA, AND COMPARISON WITH THOSE OF *C. SIGNIFERA* FROM SOUTH AUSTRALIA

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### Summary

LITTLEJOHN, M. J. & WRIGHT, J. R. (1997) Structure of the acoustic signals of *Crinia glauerti* (Anura: Myobatrachidae) from south-western Australia, and comparison with those of *C. signifera* from South Australia. *Trans R. Soc. S. Aust.* 121(3), 103-117, 28 November, 1997.

Advertisement calls of 51 males of the Australian myobatrachid frog, *Crinia glauerti*, from five sites, and 45 males of the presumed cognate species *C. signifera* from four sites, were analysed and compared. Patterns of geographical variation in the advertisement calls of *C. glauerti* were explored and a cline was found in pulse rate. The structure and geographical variation in frequency of occurrence of another signal, the squelching call, of unknown function, in the acoustic repertoire of *C. glauerti*, were investigated. The findings are consistent with the earlier reports of more frequent occurrence of the squelching call in the south. Because of possible similarity in function, the squelching call of *C. glauerti* was compared with the encounter call of *C. signifera*.

KEY WORDS: *Crinia glauerti*, *Crinia signifera*, advertisement call, encounter call, acoustic analyses, pulse structure, spectral composition, geographical variation.

### Introduction

The commonly produced call (= advertisement call, *sensu* Littlejohn 1977; Wells 1977) of the endemic south-western Australian species *Crinia glauerti* (Loveridge) was subjectively described by Main (1957) as: "A prolonged rattling call." Main (1957) also noted; "Adjacent to Perth the call of this species is constant and is predominantly a rattle, but occasionally a short squelching sound is made. On the south coast ... [away from related species], the squelching call is far more prominent ... ." This observation of inter-population variation in the calls of *C. glauerti* was considered by Brown & Wilson (1956) as a possible example of character displacement, with the squelching calls being more frequent in the populations that were allopatric to *C. insignifera* (Moore), a species which also has a squelch-like call (see Littlejohn 1959).

Although some values were cited by Brown & Wilson (1956) from A.R. Main (in litt., based on analyses by M.J. Littlejohn), the first published objective description, which included an oscillogram (= waveform) and an audiospectrogram, of the rattling call of *C. glauerti* was provided by Littlejohn (1959). This account was derived from the physical analysis of magnetic tape recordings of the calls of 12 males obtained at only one locality, South Perth (115°52' E, 31°59' S), near the northern limit of

geographic distribution (Littlejohn unpub.), so that there was no consideration of geographic variation in call structure within this species. Littlejohn (1959) also noted "occasional call variation in the form of a compressed series of pulses" which may be equated to the squelching call of Main (1957) and an oscillogram of one of these pulse trains was presented.

The disjunct allopatric south-eastern Australian taxon *C. signifera* (Girard) is presumed to be the cognate (sister) species of *C. glauerti*, with which it constitutes the *signifera* superspecies (Main 1957; Main *et al.* 1958). The advertisement call of this taxon is a short, rapidly repeated pulse train and the first published objective description, and an oscillogram, were provided by Littlejohn (1958). Littlejohn (1959, 1961) supported the proposed affinity of *C. glauerti* and *C. signifera*, on the basis of the much lower pulse rates of the advertisement calls, when compared with those in calls of the then recognized members of the related *insignifera* superspecies (Main 1957; Main *et al.* 1958). Quantitative descriptions of the calls of *C. signifera* were also provided by Littlejohn (1964, 1970), Littlejohn & Martin (1965), Hawe<sup>1</sup>, Littlejohn *et al.* (1985) and Odendaal *et al.* (1986). Interpopulation variation in advertisement calls of *C. signifera* was considered by Littlejohn (1959, 1964), and by Odendaal *et al.* (1986). Straughan and Main (1966), through choice playback experiments in which tape-recorded advertisement calls of *C. signifera* and *C. parinsignifera* (Main) were offered as alternative stimuli, demonstrated that breeding females of *C. signifera* exhibited positive phonotaxis only to the conspecific calls. Encounter calls (*sensu* Wells 1977)

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<sup>1</sup> HAWE, S. M. (1970) Calling behaviour and Territoriality in Males of Two species of *Crinia* (Anura: Leptodactylidae). BSc (Hons) thesis, Department of Zoology, University of Melbourne (unpub.).

(= territorial calls, Littlejohn *et al.* 1985) of *C. signifera* were identified through field playback experiments by Hawe<sup>1</sup> and Littlejohn *et al.* (1985). The squelching calls of *C. glauerti* may also have a territorial function but this has yet to be determined. In the absence of experimental documentation, the term "squelching call" (Main 1957) will be retained for the compressed series of pulses.

Tape-recorded samples of advertisement calls of 51 individuals were obtained at five localities across the geographic range of *C. glauerti* (Fig. 1, Table 1) to provide a measure of geographical variation. Mundaring Weir (Site 1) is the type locality for *C. glauerti* (Cogger *et al.* 1983). Squelching calls were

produced in the recorded sequences of 25 of these individuals. Sufficient squelching calls were obtained to provide a preliminary description of this type of signal for comparison with the conspecific advertisement call, and with the encounter calls of *C. signifera*, and to allow an estimation of geographical variation in the frequency of production relative to the advertisement call. Tape recordings of advertisement calls of 45 individuals from the closest populations of *C. signifera* were also obtained, namely from four localities in southern South Australia (Fig. 2, Table 1) at or near the western limits of the extensive geographic distribution of this species (see maps given by Brook 1983, 1984; Tyler

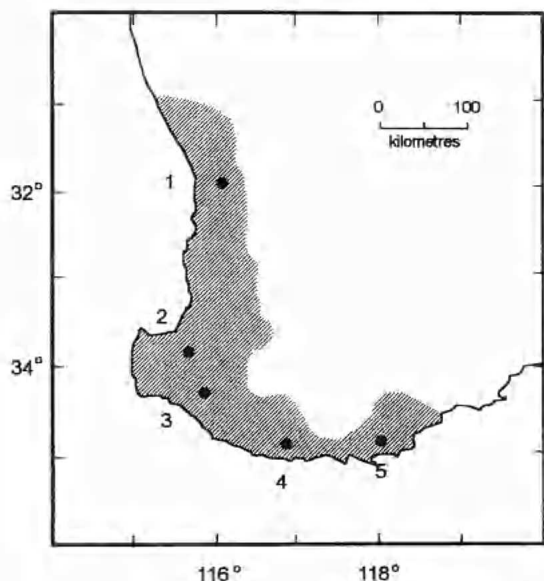


Fig. 1. Geographic distribution (based on Tyler *et al.* 1994) of *Crinia glauerti*, and locations of recording sites (see Table 1).

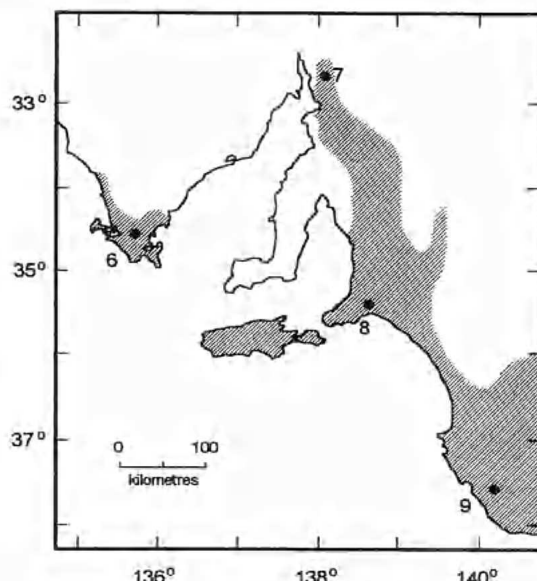


Fig. 2. Geographic distribution (based on Brook 1984) of *Crinia signifera* in South Australia and locations of recording sites (see Table 1).

TABLE 1. Details of recording localities.

All sites are in Western Australia for *Crinia glauerti* and in South Australia for *C. signifera*.

Species	Site	Dates of recording	Locality	Latitude (South)	Longitude (East)
<i>C. glauerti</i>	1	19, 23.vii.89	Helena River, at base of Mundaring Weir	31°57'	116°10'
	2	06.vii.86, 31.vii.89	21 km south-south-west of Busselton	33°51'	115°19'
	3	23.vii.86, 02.viii.86	Diamond Tree railway siding	34°22'	116°06'
	4	24, 25.vii.86	3 km east of Nornalup	34°59'	116°50'
	5	09, 10.viii.89	13 km east-north-east of Albany	34°59'	118°00'
<i>C. signifera</i>	6	18.viii.86; 15.viii.89	9.3 km south of Wanilla	34°36'	135°40'
	7	03, 04.vii.89	Yellowman Creek, 3.6 km south-east of Melrose	32°51'	138°13'
	8	28, 29.vii.90	9 km north-north-west of Victor Harbour	35°29'	138°36'
	9	26.vii.90	8.3 km north-north-east of Millicent	37°31'	140°23'

1985; Cogger 1992). The description of the encounter call (=territorial call) of *C. signifera* is based on accounts of Hawe<sup>1</sup> and Littlejohn *et al.* (1985, unpub.).

### Materials and Methods

#### Recording of calls

Tape recordings were obtained at the breeding sites (Figs 1, 2, Table 1) with an open-reel recorder (Nagra IV-S) and a cardioid dynamic microphone (Beyer M 88). Males of both species call from a variety of sites: on the banks adjacent to water, while sitting in shallow water, or while floating and supported by emergent vegetation. The effective temperatures at the calling sites (surface water, wet-bulb air, depending on the calling position of the frog) were then measured with an electronic (thermistor) thermometer (Takara Digimult Model D611, with sensor type SZL-64). The mean was used as the effective temperature when an individual was at the interface between air and water. Where possible, the recorded males of *C. glauerti* were collected, euthanased, preserved in Tyler's fixative (Tyler 1962), stored in 70% ethanol and lodged with the Western Australian Museum. If the specimen was preserved, the measurement of snout-urostyle length was later made with dial calipers (to 0.1 mm; rounded to 0.5 mm). Otherwise, a short plastic ruler (15 cm) was placed along the dorsal surface of the living specimen held in a thin, clear plastic bag, and the snout-urostyle length determined to the nearest 0.5 mm.

#### Acoustic analysis of recordings

For acoustic analysis, tape recordings were replayed on an open-reel tape recorder (Revox B 77 MkII or Sony TC-510-2). Advertisement calls were analysed by using a digital audio-spectrograph (Kay Elemetrics Model DSP-5500 Sona-Graph). Where there were high levels of low-frequency noise, a passive filter (Allison 2B, high pass, cut-off set at 512 Hz) was inserted between the output of the tape recorder and the input of the audio-spectrograph. Statistical procedures were carried out with SYSTAT, Version 5.03 (Systat Inc., Evanston).

#### Characteristics of equipment used in recording and analysis

Tape transport speeds ( $19 \text{ cm s}^{-1}$ ) of the recorders involved in recording and playback were periodically checked against a locally produced standard 1000 kHz calibration tape and a frequency counter (Heath Schlumberger SM-118A or Good Will GFC-8010G) (Revox, Sony), or against the 50 Hz AC mains frequency by a built-in stroboscope (Nagra); overall variations in tape speed through recording and

playback are estimated to be less than  $\pm 0.5\%$ . The frequency responses of all electronic components used in recording and analysis are presumed to be close to linear within the narrow range of frequencies of interest (c. 2.0 - 5.0 kHz), based on manufacturers' specifications. The relatively high sampling rates used in the digital analyses ( $>44 \text{ kHz}$ ) preclude the production of artifacts from aliasing.

#### Structure and acoustic attributes of calls

The calls of the two species are of simple structure and each consists of a group of discrete damped oscillations (Figs 3-5). For convenience, and following previous usage, each of these oscillations is referred to as a "pulse," and the group (i.e. the pulse train) as a call (Figs 3, 4). The number of pulses in a call was determined by direct inspection of the displayed waveform. The depth of amplitude modulation of the last two pulses in a call was sometimes less than 100%; in such cases, separate pulses were recognized if the depth of modulation exceeded about 75%. The duration (to nearest ms) of a call was taken as the interval from the peak of the first pulse to the peak of the last pulse (= "peak-peak duration"). The pulses in the advertisement calls are produced in a quasi-periodic fashion, and the pulse rate (as  $\text{p s}^{-1}$ ) was calculated over a complete call as  $(n - 1 \text{ pulses}) \times 1000/\text{peak-peak duration in ms}$ . Dominant frequencies were measured as the peaks in a power spectrum of the whole call. To describe the temporal and spectral properties of pulses in advertisement calls, a tape recording of one call of each of three individuals of each species (*C. glauerti*,

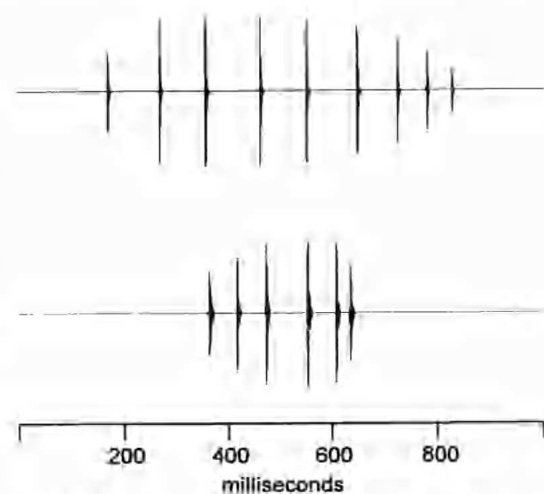


Fig. 3. Waveforms of advertisement calls. Upper, *Crinia glauerti*; Reference R439-7, Site 1; effective temperature, wet-bulb air =  $11.8^\circ \text{ C}$ . Lower, *C. signifera*, Reference R408-2, Site 6; effective temperature, wet-bulb air =  $11.1^\circ \text{ C}$ , water =  $12.5^\circ \text{ C}$ .

Site 1; *C. signifera*, Site 6) was replayed into a digital sound card (Sound Blaster SB16, Creative Labs Milpitas), installed in a desktop computer (IBM-PC compatible). The sampling rate was set at 44,100 Hz and the sample size at 16 bits. Files were prepared in the WAVE format with the Creative WaveStudio Version 2.0 software (Creative Technology Singapore), and further processed with this package and with Spectra Plus Professional, Version 3.0 (Pioneer Hill Software Poulsbo). The figures of the waveforms and spectra (Figs 3-5) were prepared by the same procedure. One pulse (the middle pulse or next after the midpoint of a call if an even number) of each call was used for analysis.

Conventional rise and decay times of pulses (from 10 - 90%, and 90-10%, respectively, of maximum amplitude) were not calculated because it would have been necessary to extrapolate between peaks of the carrier frequency (see below). Accordingly, the number of either positive or negative half cycles to reach maximum amplitude was counted and the time interval from background noise level to the peak

estimated. The pulse duration was measured as the interval from approximately 10% of the maximum amplitude (either positive or negative) at the start to the same level at the end of a pulse. Two dominant spectral peaks are present in most of the calls of both species (Fig. 4). There is a well-defined sinusoidal fundamental frequency within the wave train (Fig. 4) and this is referred to as the carrier frequency (CF), by analogy with amplitude modulation in electronics.

Rates of production of advertisement call were determined by playback of original recordings on a Sony TC-510-2 recorder. For *C. glauerti*, the durations of five consecutive cycles of calls and intervals were measured; for *C. signifera*, 10 cycles were measured. The following protocols were employed to arrive at the sequences of calls selected for measurement: *C. glauerti* - the first six clear calls in the recorded sequence; *C. signifera* - the last 16 calls in the sequence were digitised, then the last five discarded. The interval from the end of the first call to the end of the sixth (*C. glauerti*) or tenth (*C.*

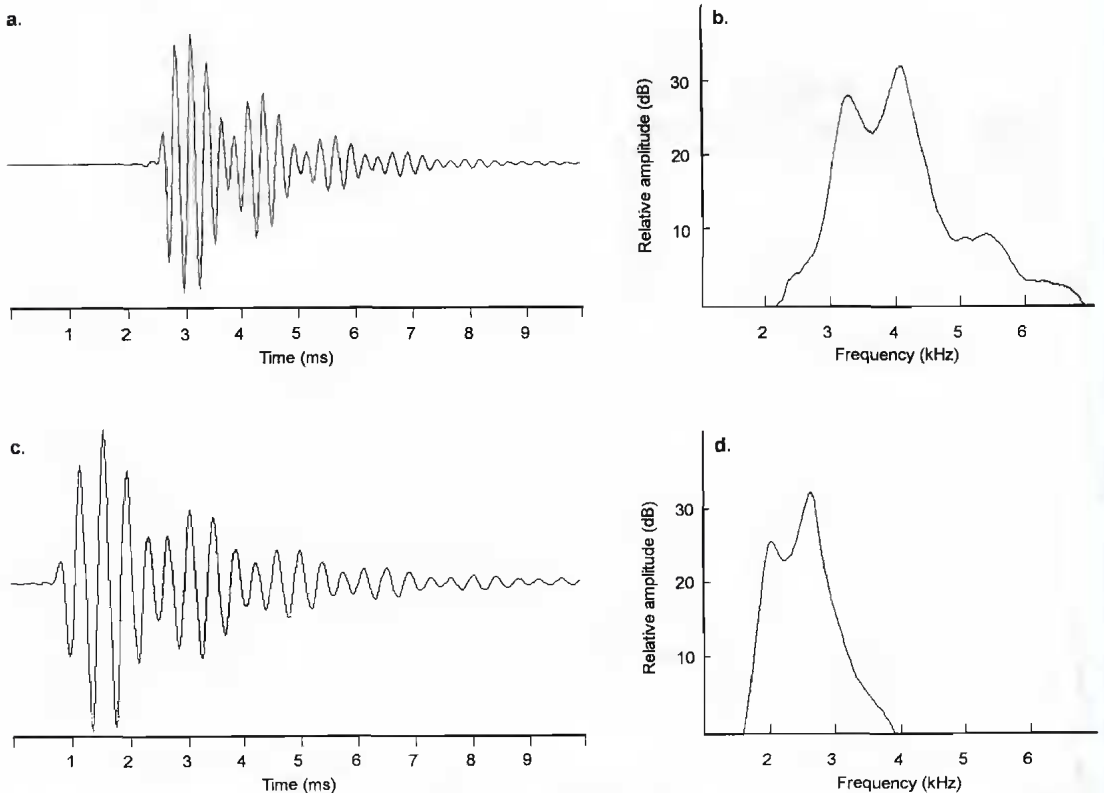


Fig. 4. Structure of pulses in advertisement calls. Upper panels. (a). Expanded waveform. (b). Frequency spectrum for *Crinia glauerti* (Reference: R439-9, Site 1; effective temperature = 12.2° C). Lower panels. (c). Expanded waveform. (d). Frequency spectrum for *C. signifera* (Reference: R408-5, Site 6; effective temperatures, wet bulb air = 10.9° C, water = 12.7° C).

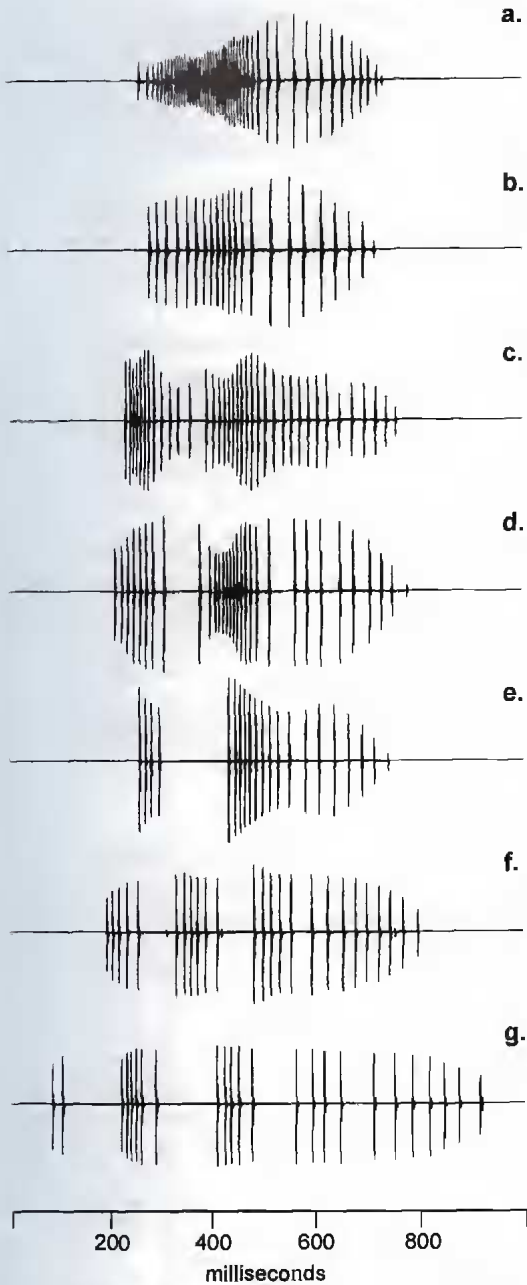


Fig. 5. Waveforms of squelching calls of *Crinia glauerti*. (a). R441-5, Site 5, effective temperature = 11.8° C. (b). R441-1, Site 5, effective temperature = 13.1° C. (c). R404-2, Site 2, effective temperature = 9.6° C. (d). R441-4, Site 5, effective temperature = 13.1° C. (e). R407-6, Site 3, effective temperature = 11.1° C. (f). R404-3, Site 3, effective temperature = 9.8° C. (g). R407-7, Site 3, effective temperature = 10.7° C.

a. *signifera*) call was then measured to the nearest millisecond.

#### Numbers of advertisement calls of individuals analysed

The number of advertisement calls of each individual to be analysed was determined as follows. Both species produce advertisement calls in long and regular sequences. In *C. glauerti*, production of the longer advertisement calls is slow - about 20% of the rate of *C. signifera* (see below). For *C. glauerti*, as the first step, four clear calls of each individual ( $n = 10$ ) from Site 1 were chosen at random from the recorded sequence. If four clear calls could not be obtained, that individual was discarded from the analysis. For *C. signifera*, all individuals from Site 8 ( $n = 10$ ) were used and data were obtained from three successive calls: the 12th, 13th and 14th (or the nearest clear call if there was an overlap) from the start of a natural sequence, or after recording had commenced. For each attribute of the call and for each species, an analysis of variance was carried out with comparison between individuals. The variance was partitioned and the proportion of the variation due to within-individual effects and that due to between-individual effects was calculated. For both species and all variables, variation between individuals was far greater than that within individuals. For *C. glauerti*, the within-individual variation accounted for 13-20% of the variation in the data. For *C. signifera*, the within-individual variation accounted for 24-25% of the variation. Based on these results of the analyses of variance, it was decided that for *C. glauerti*, the average of two calls per individual would provide a representative sample for that individual. As the calls of *C. signifera* were slightly more variable, it was decided to use the average of three calls for each individual. Mean values for individuals are used in the subsequent treatment of these data.

#### Effects of temperature

Linear regression analyses of the full data set for advertisement calls (Table 2) indicated that for *C. glauerti* there was a significant ( $p < 0.05$ ) relationship between effective temperature and duration and between effective temperature and pulse rate. The linear regression analyses also indicated that there was a significant relationship between dominant frequency and effective temperature for advertisement calls of each species. Accordingly, values of the dependent variables were corrected to 11.0° C, the nearest integer to the pooled mean for effective temperature (*C. glauerti*, mean = 11.1° C; *C. signifera*, mean = 10.8° C); these values were used in subsequent calculations. Where the slope for the combined samples for each species was non-significant, the raw data were used in

TABLE 2. Influence of effective temperature on four attributes of the advertisement calls of *Crinia glauerti* ( $n = 51$ ) and *C. signifera* ( $n = 45$ ).

Results of analyses by linear regression. See Table 4 for ranges of temperatures.

Attribute of call	Species	Slope	Significance of slope ( $p$ )	Coefficient of determination ( $r^2$ )
Duration	<i>C. glauerti</i>	-0.070	<0.001	0.291
	<i>C. signifera</i>	+0.013	0.240	0.032
Number of pulses	<i>C. glauerti</i>	-0.151	0.516	0.009
	<i>C. signifera</i>	+0.290	0.141	0.050
Pulse rate	<i>C. glauerti</i>	+1.448	<0.001	0.239
	<i>C. signifera</i>	+0.499	0.587	0.007
Upper dominant frequency	<i>C. glauerti</i>	-100.107	0.008	0.134
	<i>C. signifera</i>	-156.566	<0.001	0.249

the subsequent analyses.

#### Occurrence of squelching calls of *C. glauerti*

The presence of squelching calls was determined subjectively, by replaying the tape-recorded sequences of each individual. In this analysis, three types of call were recognised: advertisement calls, squelching calls, and transitional calls - as it was not possible to assign some to either category. The squelching calls of *C. glauerti* also consist of pulse trains (Fig. 5). Because these calls are highly variable in temporal structure, and were produced only during the recorded sequences of about 50% of the individuals, they are only briefly described in a subjective way.

## Results

#### Structure of pulses in advertisement calls

The pulses in calls of both species are similar, each with a sharp attack and a gradual (negative exponential) decay (Fig. 4). Estimated durations are 4 ms for *C. glauerti* and 4-7 ms for *C. signifera*. The maximum amplitude is reached within three positive or negative peaks of the carrier frequency, that is, in about 1 ms for both taxa. Examination of the expanded wave form of each pulse indicated the presence of a clear sinusoid (= fundamental/carrier) with a frequency that is close to the upper peak of the spectrum (Table 3). Accordingly, only the upper peak (= carrier frequency) was used in subsequent calculations. The frequency bandwidth at 10 dB

below the peak is about 1200 Hz for both species (Fig. 4). The envelope of the pulse is amplitude modulated to a depth of about 30-60% (based on the first cycle) with the envelope modulating frequency (EMF) within a range of 694 to 820 Hz for *C. glauerti*, and of 505 to 885 Hz for *C. signifera* (Fig. 4). These values are close to the difference between the upper and lower peak of the spectrum for each individual (Fig. 4, Table 3). It is suggested that the lower peak that is present in the spectrum of the advertisement calls of some individuals of each species (Fig. 4) is a sideband of the carrier frequency (i.e. the upper dominant frequency). The level of the lower peak is about 4-9 dB below that of the upper peak (Table 3).

#### Structure of the advertisement calls

Both species produce advertisement calls in long and regular sequences. For *C. glauerti* from Site 1, calls were produced at a mean rate of 26.5 calls  $\text{min}^{-1}$  (range = 22.9 - 28.8;  $n = 9$ ) at a mean effective temperature of 12.1° C (range = 11.4 - 12.8). For *C. signifera* from Site 8, the mean rate was 124.7 calls  $\text{min}^{-1}$  (range = 81.1 - 187.1;  $n = 11$ ) at a mean effective temperature of 11.4° C (range = 11.2 - 11.7). Values for three primary attributes (duration, number of pulses and carrier frequency) and the one derived attribute (pulse rate) for five samples of *C. glauerti* and four samples of *C. signifera*, corrected for the effect of temperature where appropriate, are

TABLE 3. Spectral characteristics of pulses in advertisement calls of *Crinia glauerti* and *C. signifera*. All values are in Hz. See text for explanation.

Species	Individual	Carrier frequency (CF)	Envelope modulation frequency (EMF)	Lower spectral peak (LSP)	Upper spectral peak (USP)	Difference between spectral peaks (DSP = USP - LSP)	Difference between CF and USP	Difference between EMF and DSP
<i>C. glauerti</i>	1	4065	820	3370	4048	678	17	142
	2	4167	694	3472	4134	662	33	32
	3	4049	820	3266	4048	782	1	38
<i>C. signifera</i>	1	2494	505	2050	2497	447	3	58
	2	2632	671	2068	2670	602	38	69
	3	3413	885	2454	3445	991	32	106

TABLE 4. Physical characteristics of advertisement calls of *Crinia glauerti* and *C. signifera*, corrected to an effective temperature of 11.0 °C, where appropriate (see Table 2).

For each cell, the mean and standard deviation are given on the upper line, and range (in parentheses) on the lower line.

Species	Site	Sample size	Effective temperature (°C)	Call duration (ms)	Number of pulses	Pulse rate (p s <sup>-1</sup> )	Carrier frequency (Hz)
<i>C. glauerti</i>	1	10	12.17, 0.47 (11.4 - 12.8)	738, 87 (573 - 817)	9.70, 1.21 (7.5 - 11.5)	11.80, 1.94 (9.4 - 16.3)	4052, 229 (3584 - 4430)
	2	9	10.14, 0.64 (9.2 - 11.0)	724, 153 (552 - 982)	9.83, 1.50 (8.0 - 12.0)	12.66, 0.56 (12.0 - 13.6)	4279, 285 (3580 - 4540)
	3	13	10.27, 1.03 (7.7 - 11.5)	705, 115 (547 - 935)	11.50, 1.88 (9.0 - 15.5)	14.94, 1.80 (11.8 - 18.3)	4068, 215 (3770 - 4530)
	4	8	10.56, 0.57 (9.6 - 11.4)	526, 82 (438 - 655)	10.06, 1.84 (8.5 - 13.0)	16.91, 1.48 (14.2 - 18.6)	4031, 485 (3250 - 4570)
	5	11	12.27, 0.62 (11.0 - 13.1)	598, 85 (486 - 747)	11.23, 2.37 (8.0 - 16.0)	18.20, 2.90 (15.1 - 23.3)	4076, 292 (3640 - 4450)
	Combined sample	51	11.10, 1.18 (7.7 - 13.1)	664, 130 (438 - 982)	10.57, 1.92 (7.5 - 16.0)	14.93, 3.06 (9.4 - 23.3)	4098, 302 (3250 - 4570)
<i>C. signifera</i>	6	12	11.54, 0.54 (10.4 - 12.2)	272, 77 (150 - 437)	6.28, 1.54 (4.0 - 10.3)	19.68, 3.41 (15.5 - 28.8)	2790, 325 (2504 - 3568)
	7	13	10.64, 0.78 (9.2 - 11.2)	161, 70 (91 - 272)	5.31, 1.41 (4.0 - 9.0)	29.05, 7.56 (18.4 - 43.8)	2431, 241 (2092 - 2871)
	8	10	11.43, 0.18 (11.2 - 11.7)	182, 55 (101 - 237)	4.87, 0.69 (4.0 - 6.0)	22.50, 4.53 (17.5 - 29.7)	2569, 87 (2471 - 2710)
	9	10	9.25, 0.27 (8.9 - 9.8)	158, 20 (125 - 192)	4.37, 0.48 (4.0 - 5.0)	21.32, 1.91 (18.2 - 24.1)	2825, 169 (2549 - 3103)
	Combined sample	45	10.75, 1.02 (8.9 - 12.2)	195, 77 (91 - 437)	5.26, 1.34 (4.0 - 10.3)	23.38, 6.15 (15.5 - 43.8)	2645, 279 (2092 - 3568)

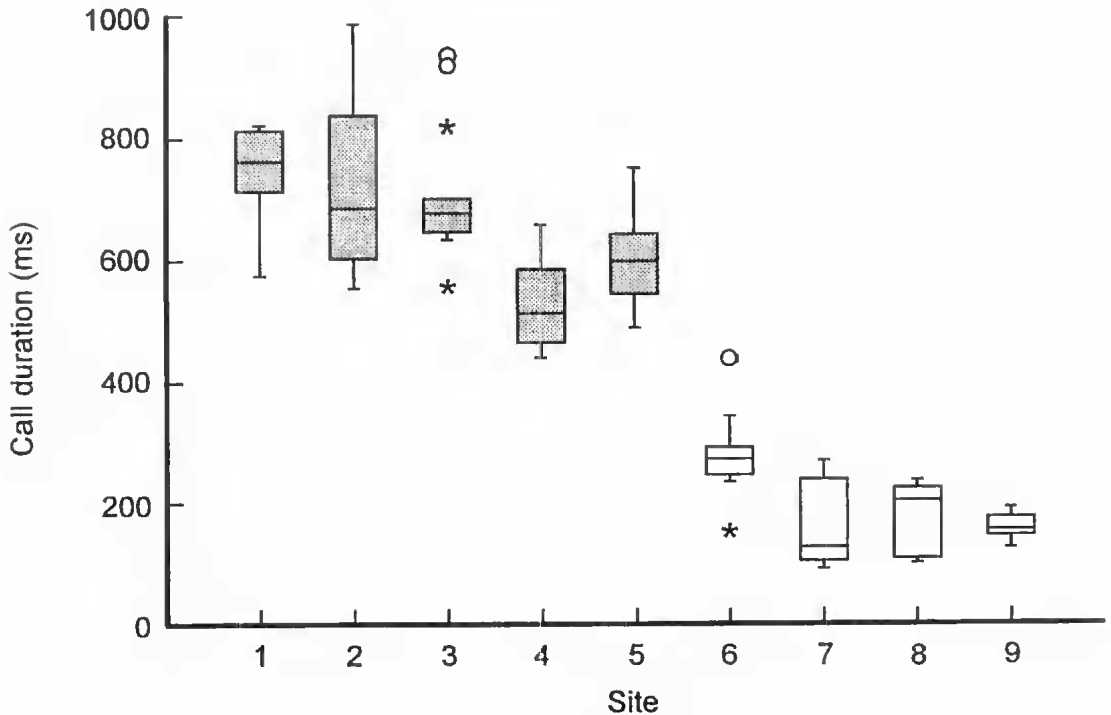


Fig. 6. Box plots for durations of advertisement calls at recording sites of *Crinia glauerti* (hatched boxes) and *C. signifera* (open boxes). Values are corrected to 11 °C where slopes are significant. The box indicates the interquartile range and the included horizontal line is the median. The vertical lines outside the boxes (whiskers) connect to the last data points within  $\pm 1.5 \times$  the interquartile range (the fences). The asterisks indicate outliers (values lying between  $\pm 1.5$  and  $3.0 \times$  the interquartile range) and the open circles indicate extreme outliers (values beyond  $3 \times$  the interquartile range).

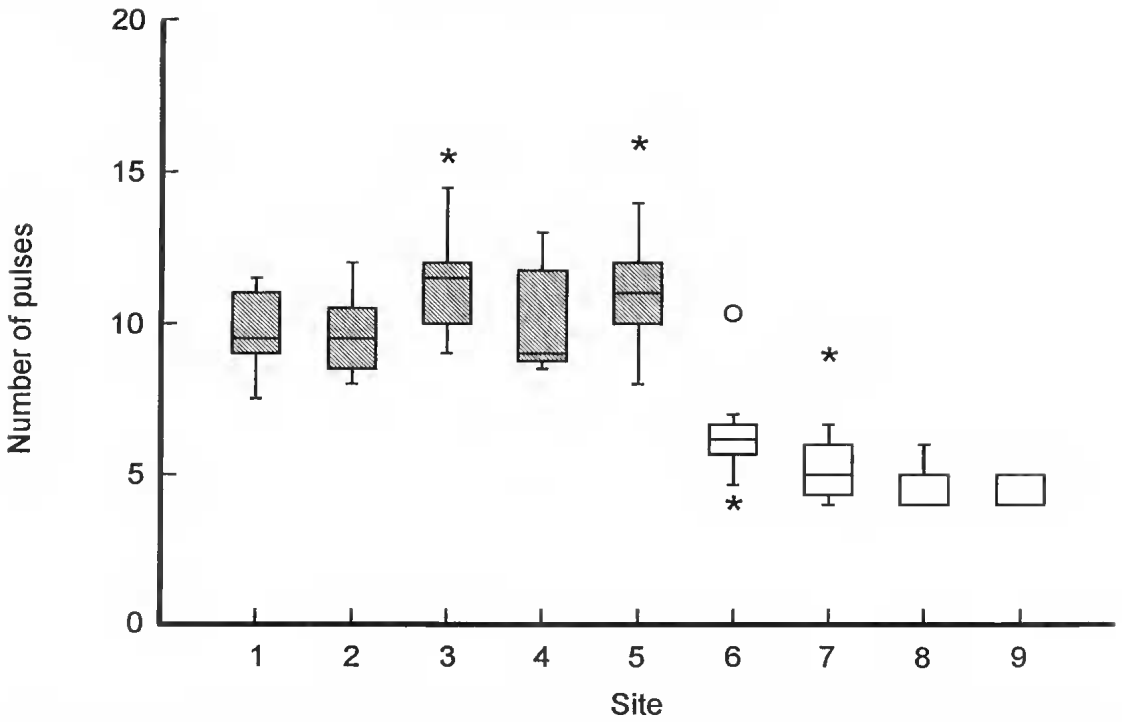


Fig. 7. Box plots for numbers of pulses in advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. See Fig. 6 for explanation.

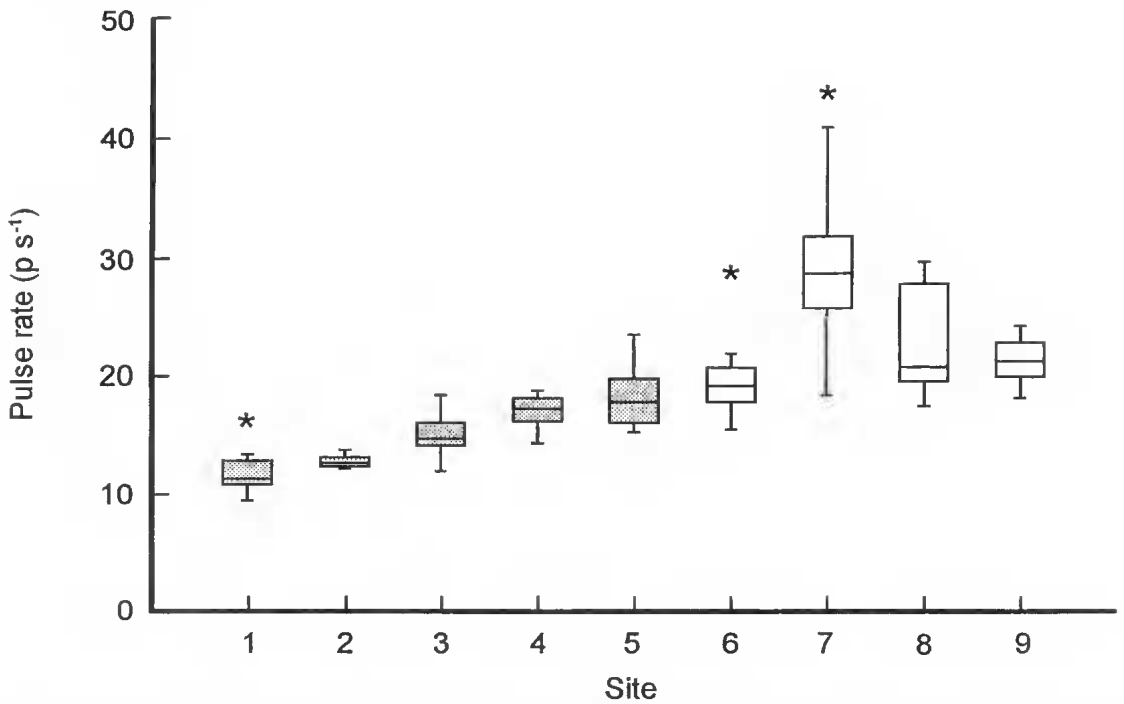


Fig. 8. Box plots for pulse rates of advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. Values are corrected to 11°C where slopes are significant. See Fig. 6 for explanation.



presented in Table 4. Values for combined samples of each species are also presented in Table 4. Box plots of these values at each site are presented in Figs 6-9.

*Correlations of attributes of advertisement calls with body length*

Calling males of *C. glauerti* are smaller than those of *C. signifera* (Table 5), with mean snout-urostyle lengths of 16.31 (range = 14.0-19.0; n = 29), and 21.31 (range = 18.0-25.0; n = 16) mm respectively (t-test;  $p < 0.001$ ). There is no significant correlation of carrier frequency (corrected

to 11.0° C; Table 2) with snout-urostyle length when all collected specimens of *C. glauerti* are included ( $r = -0.297$ ;  $p = 0.118$ ; n = 29); but there is a significant negative correlation when only those specimens that were measured following preservation are considered ( $r = -0.440$ ;  $p = 0.032$ ; n = 24). For *C. signifera*, however, there is a highly significant negative correlation between carrier frequency and snout-urostyle length ( $r = -0.796$ ;  $p > 0.001$ ; n = 16, all specimens were alive when measured). A scattergram of the correlation of snout-urostyle length and carrier frequency is presented in Fig. 10.

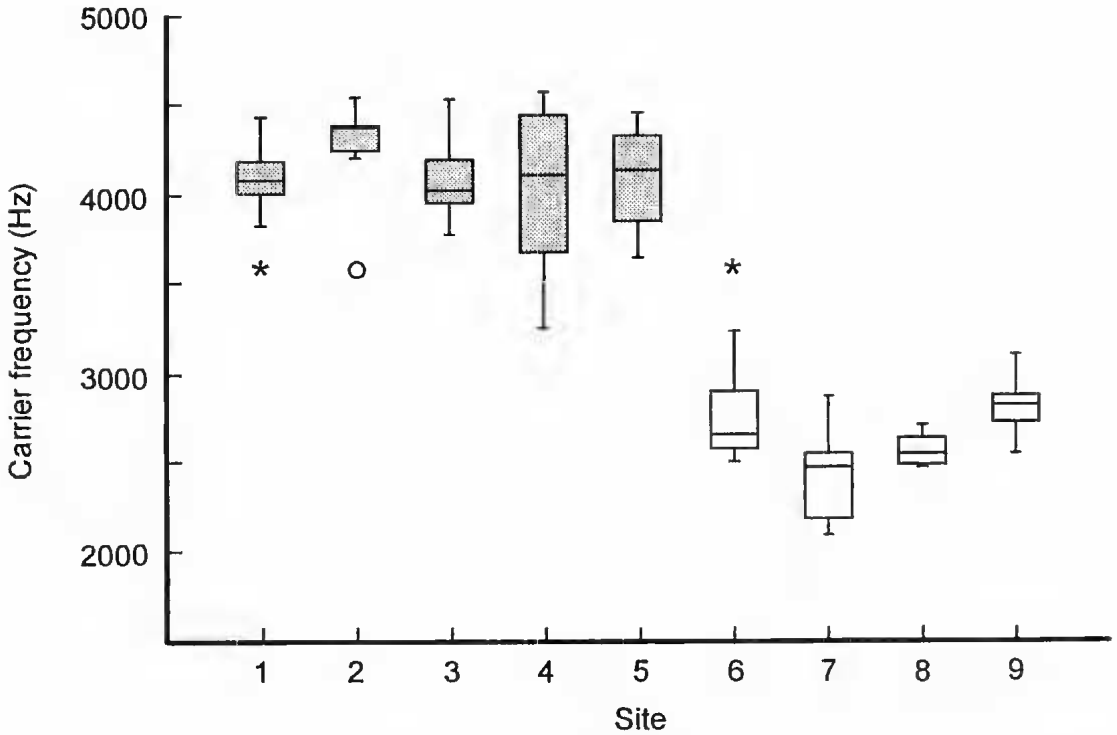


Fig. 9. Box plots for carrier frequencies of advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. Values are corrected to 11° C where slopes are significant. See Fig. 6 for explanation.

TABLE 5. Values (in mm) for snout-urostyle lengths of males of *Crinia glauerti* and *C. signifera* collected after their advertisement calls had been recorded.

Species	Site	Sample size	Mean	Range	Standard deviation	Condition of specimen
<i>C. glauerti</i>	1	8	17.2	16.5 - 19.0	0.80	preserved
	2	6	14.6	14.0 - 15.5	0.58	preserved
	3	7	16.2	15.5 - 17.0	0.49	preserved
	4	3	15.5	15.0 - 16.0	0.50	preserved
	5	5	17.6	17.0 - 18.0	0.55	live
	Total	29	16.31	14.0 - 19.0	1.25	
<i>C. signifera</i>	8	7	23.4	22.0 - 25.0	1.17	live
	9	9	19.7	18.0 - 21.0	1.41	live
	Total	16	21.31	18.0 - 25.0	2.31	

*Geographical variation in advertisement calls of C. glauerti*

Analysis of variance, with Site as the grouping factor, indicated that there are no significant differences for number of pulses ( $p = 0.074$ ) and carrier frequency ( $p = 0.411$ ). There are, however, significant differences for the means (adjusted to 11° C) of duration ( $p < 0.001$ ) and pulse rate ( $p < 0.001$ ). Across the distance of about 450 km covered by the five sites (Fig. 1), there is no consistent trend in duration (Fig. 6, Table 4), although a multiple comparison (Tukey test) indicated that the means for Sites 1-3 are significantly lower than those at Site 4, and Site 1 also differed from Site 5. There is a cline of increasing values for pulse rates (Fig. 8, Table 4). A Tukey test showed that the following means for pulse rate differ significantly: Site 1 from Sites 3, 4, and 5; Site 2 from Sites 4 and 5; and Site 3 from Site 5.

*Geographical variation in advertisement calls of C. signifera*

Sites 7, 8 and 9 are within the continuous distribution of *C. signifera* (see maps given by Brook 1983; Tyler 1985) and are spaced at about 300 km intervals. Site 6 is in the isolate on Eyre Peninsula and about 300 km from Sites 7 and 8 (Fig. 2).

Analyses of variance, with Site as the grouping factor, indicated that there were significant differences for all four attributes of the calls ( $p \leq 0.003$ ). Multiple comparisons (Tukey test) revealed the following significant differences in means between sites: call duration - Site 6 from Sites 7-9; pulse number - Site 6 from Sites 8 and 9; dominant frequency (adjusted to 11° C) - Site 7 from Sites 6 and 9; pulse rate - Site 7 from Sites 6, 8 and 9.

*Comparison of advertisement calls of C. glauerti and C. signifera*

Results of analyses of variance, with Species as the grouping factor, indicated that the advertisement calls of the two species differed significantly ( $p < 0.001$ ) in all four attributes. From a consideration of the combined samples for each species (Table 4), calls of *C. glauerti* are much longer, with means of durations differing by 3.4 times, and with no overlap in ranges of variation (Fig. 6). The mean value for number of pulses in advertisement calls of *C. glauerti* is twice that of *C. signifera* but there is an overlap of ranges between 7.5 and 10.3 (Fig. 7, Table 4). For pulse rates, although the mean for *C. glauerti* is only 64% of that for *C. signifera*, the ranges overlap extensively (Fig. 8, Table 4), particularly for the closest samples (Sites 5, 6). The mean for carrier

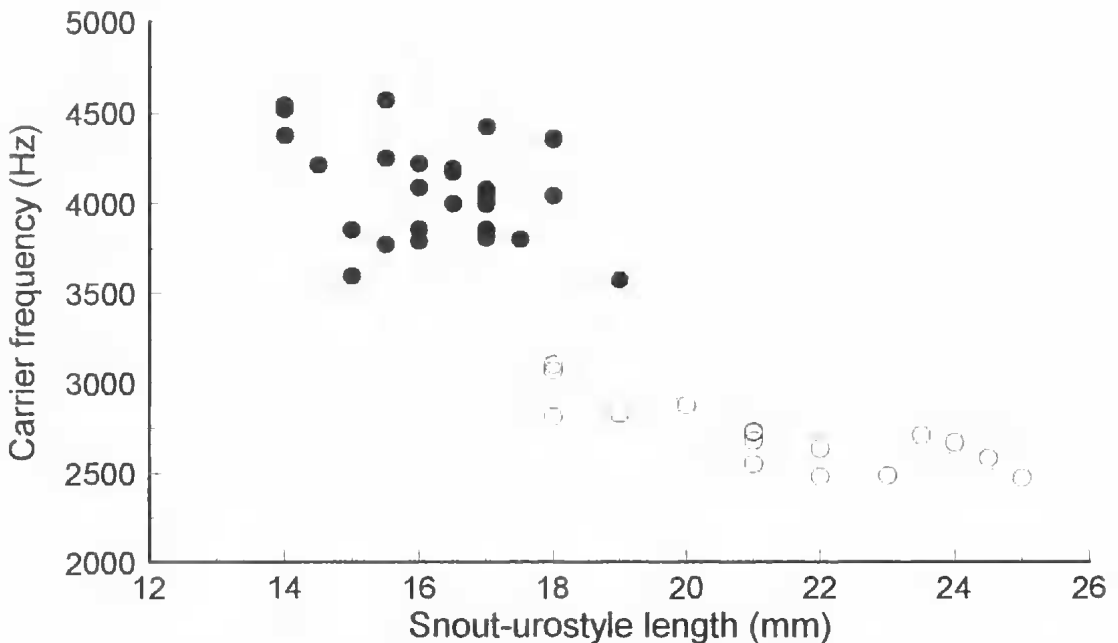


Fig. 10. Scattergram showing the correlation between carrier frequency and snout-urostyle length for males of *Crinia glauerti* and *C. signifera* that were collected after their calls had been recorded.

TABLE 6. Physical characteristics of seven squelching calls of *Crinia glauerti*; from the same set of calls presented in Figure 5.

Individual (and tape reference)	Temperature (°C)	Duration (ms)	Number of pulses	Low pulse rate (p s <sup>-1</sup> )	High pulse rate (p s <sup>-1</sup> )	Overall pulse rate (p s <sup>-1</sup> )	Carrier frequency (Hz)
a. (R441-5)	11.8	475	50	43.2	205.9	103.2	3703
b. (R441-1)	13.1	438	22	31.1	79.0	48.0	3746
c. (R404-2)	9.6	524	37	46.7	125.0	68.7	4392
d. (R441-4)	13.1	569	31	36.3	137.2	52.7	4230
e. (R407-6)	11.1	478	21	37.4	92.3	41.8	4220
f. (R404-3)	9.8	603	25	40.2	61.7	39.8	4263
g. (R407-7)	10.7	832	24	29.7	105.3	27.6*	4048
Means	11.31	559.9	30.0	37.80	115.20	54.55	4086
Ranges	9.6-13.1	438-832	21-50	29.7-46.7	61.7-205.9	27.6-103.2	3703-4392

\*lower than low pulse rate because of the four long breaks in the train.

frequencies is higher in *C. glauerti*, by 1452 Hz, but with an overlap of ranges between 3229 and 3568 Hz (Fig. 9, Table 4).

#### Structure of the squelching call of *C. glauerti*

These calls are highly variable, as is indicated by the selection of waveforms presented in Fig. 5. The pulses are sometimes in groups within a call, and the pulse rate can vary greatly through a call (Fig. 5). Values for four attributes of the seven calls presented in Fig. 5 are given in Table 6. The pulses are of similar structure to those of the advertisement call and there are also two peaks in the frequency spectra, as in the advertisement call. For the seven calls presented in Fig. 5, the following data apply (see section on pulses of advertisement calls for methodology): duration - mean = 3.77 ms (range = 3.1 - 5.1); carrier frequency - mean = 3955 Hz (range = 3481 - 4427); upper frequency peak - mean = 3976 Hz (range = 3703 - 4414); envelope modulating frequency - mean = 877 Hz (n = 5; range = 735 - 1062); lower dominant frequency peak - mean = 3260 Hz (n = 5; range = 3100 - 3464). The difference between the means of peaks of upper and lower frequencies of 716 Hz is consistent with the explanation advanced for the pulses in the advertisement calls - of the lower sideband of an envelope modulating frequency. The pulses may be grouped within a call (Fig. 5) and the pulse rates can differ considerably between groups in one call (Table 6).

#### Geographical variation in frequency of occurrence of the squelching call of *C. glauerti*

Recorded sequences of calling by 25 of the 51 individuals included squelching calls. Because of confusion from the calling by two or more close individuals, only those of 21 could be reliably assessed, classified and counted (Table 7). A geographical trend is evident, with the frequency of production of squelching calls by individuals being higher in the southern and south-eastern samples

(Sites 4, 5, Table 8). No attempt was made to determine the extent of variation in the squelching calls of individuals, nor over time for a population.

#### Structure of the encounter calls of *C. signifera*

Littlejohn *et al.* (1985), by playback of advertisement calls of *C. parvisignifera* and *C. signifera* at peak sound pressure levels (0 dB re 20 µPa) above c. 98 and 104 dB respectively, evoked encounter calls (= territorial calls *sensu* Hawe!; Littlejohn 1977) from eight males of *C. signifera* at Willowmavin in south central Victoria (37°16' S, 144°54' E). The encounter call (Fig. 11) is also a pulse train, with a regular pulse rate (Hawe!;

TABLE 7. Numbers of advertisement calls, intermediate (transitional) calls and squelching calls, and proportions of the latter (of all calls of that individual), produced by 21 males of *Crinia glauerti*.

Note that because of overlap with neighbours, calls of 4 individuals could not be analysed.

Site	Individual	Number of advertisement calls	Number of intermediate calls	Number of squelching calls	Proportion of squelching calls
1	1	30	0	3	0.091
2	1a	12	2	7	0.33
2	2	9	1	11	0.52
3	2	18	4	4	0.15
3	3	27	3	8	0.21
3	6	20	1	7	0.19
3	7	21	4	11	0.31
4	6	13	0	7	0.35
4	8	14	2	4	0.20
4	2	10	4	4	0.22
5	1a	18	2	12	0.38
5	2a	10	5	4	0.21
5	3a	15	6	4	0.16
5	4a	24	0	1	0.04
5	5a	9	0	6	0.40
5	6	0	10	15	0.60
5	1b	11	5	6	0.27
5	2b	9	3	22	0.65
5	3b	15	1	8	0.33
5	4b	16	6	11	0.33
5	5b	10	5	13	0.46

TABLE 8. Numbers and proportions of males of *Crinia glauerti* producing squeelching calls at each site.

Site	Number of males assessed	Number of males producing squeelching calls	Proportion of males producing squeelching calls
1	10	2	0.200
2	11	3	0.273
3	12	5	0.417
4	8	4	0.500
5	11	11	1.000

Littlejohn 1977). A waveform of an encounter call from Site 5 is presented in Fig. 11. Values for means and ranges from the original data for advertisement calls and evoked encounter calls of the same five individuals discussed by Littlejohn *et al.* (1985) are presented in Table 9.

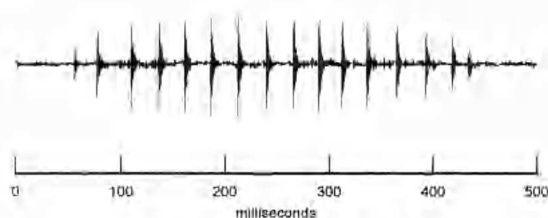


Fig. 11. Waveform of an encounter call of *C. signifera* (Reference: R408.9; Site 6; effective temperatures: wet-bulb air 11.3°C, water 12.5°C).

TABLE 9. Comparison of attributes of advertisement calls and encounter calls of *Crinia signifera* from Willowswain, Victoria (from data of Littlejohn *et al.* 1985).

Means and ranges (in parentheses) are given ( $n = 5$ ). Data are not corrected for possible effects of temperature. Effective temperatures ranged from 10.7–13.2°C (mean = 12.04).

Attribute	Advertisement call	Encounter call
Duration (ms)	83 (56–108)	192 (179–210)
Pulses/note	4.2 (4–5)	17.8 (16–19)
Pulse rate (p s <sup>-1</sup> )	40.6 (30.8–53.7)	88.1 (74.2–100.1)
Upper dominant frequency (Hz)	3390 (3125–3642)	3217 (2825–3626)

#### Production of encounter calls by males of *C. signifera*

In a subjective evaluation during playback of the tape recordings of *C. signifera*, involving 53 individuals and some 3527 advertisement calls, three interactions, presumed to involve production of encounter calls, were noted. Otherwise, the recorded sequences of 47 individuals consisted only of advertisement calls.

#### Comparison of squeelching call of *C. glauerti* and territorial call of *C. signifera*

The variable squeelching call of *C. glauerti* (Fig. 5, Table 6) is longer, contains more pulses, is of higher average pulse rate, and of higher dominant frequency than the territorial call of *C. signifera* (Fig. 11, Table 9). Even so, they are both pulse trains which are of similar carrier frequency but of longer duration, contain more pulses, and are of higher pulse rate than their respective advertisement calls (Fig. 3, Table 4).

## Discussion

#### Structure of the advertisement calls of both species

The advertisement calls of both species are of similar structure, each consisting of a quasi-periodic pulse train. The pulses are short damped oscillations, each with a sharp attack and an exponential decay. There are more pulses in the calls of *C. glauerti*, and these are produced at a lower repetition rate. The frequency spectra are of similar shape, with most individuals having two peaks, the upper being attributed to the fundamental (= carrier frequency), while the lower is presumed to be produced as the side band of the envelope modulating frequency. The carrier frequency is higher in *C. glauerti*, and this may be correlated with the smaller size of males of this species – a usual characteristic of the calls of anurans (e.g. Robertson 1986). There is a trend of increasing pulse rate from north to south-east in the samples of *C. glauerti* and the durations are lower in the samples from Sites 4 and 5. Values for samples of the other two attributes display no obvious pattern.

Advertisement calls from Site 6 in the geographical isolate of *C. signifera* on lower Eyre Peninsula are longer and contain more pulses than those to the east in the main distribution of *C. signifera*. Thus the westernmost sample of *C. signifera* (from Site 6) is more similar to those of *C. glauerti* than are the others. The populations of *C. signifera* on Eyre Peninsula have probably been separated from the main distribution since the sea rose to its present level at the close of the last glacial period of the Pleistocene Epoch (from c. 12,000 to c. 6,000 years ago; see Littlejohn *et al.* 1993 for a summary and references) and this isolation may have contributed to the divergence.

Odendaal *et al.* (1986) recorded a sample of advertisement calls of *C. signifera* from the same location on Yellowman Creek (their Recording Site No. 5; our Site No. 7) and over a comparable range of effective (water) temperatures (10.8–12.2 °C v. 9.2–11.2 °C - this study). For all four attributes, however, their values are higher than those obtained in the present study. The use of other protocols and analytical techniques may account for some of the differences, but at this stage, no explanation can be offered.

#### Frequency of encounter calls in *C. glauerti*

More-recent observations by Littlejohn (unpub.) indicated that *C. glauerti* occurs in syntopy with *C. subinsignifera* (Littlejohn) near the eastern limit of its distribution (e.g. Site 5, Fig. 1). *Crinia subinsignifera* has an advertisement call that sounds like a "long low-pitched squeelch" (Littlejohn 1957, 1959). For two temporal attributes of the advertisement calls of 37 individuals of *C. subinsignifera*, corrected to an effective temperature of 10 °C, the mean duration is 540 ms (range = 420–660), and the mean pulse rate is 174 (range = 129–210) (Littlejohn 1961). As these ranges overlap those of the squeelching call of *C. glauerti* (Table 6), explanations other than reproductive character displacement must now be sought for the higher frequencies of occurrence of squeelching calls in the south and south-east but none can be provided at present. Clearly, there is a need for further investigations, including playback experiments with advertisement calls and squeelching calls as stimuli under controlled conditions. Such studies should be preceded by the documentation of frequency of occurrence of squeelching calls in natural assemblages, and the context in which they are produced. The measurement of the sound pressure levels of calls of conspecific neighbours is also required so that the appropriate stimuli can be applied (Littlejohn *et al.* 1985). By varying the levels of stimulation, thresholds could then be determined and geographical patterns may be revealed.

#### Relationships of *C. glauerti*

From the presented data, it appears that the nearest populations of *C. glauerti* and *C. signifera* (Sites 5, 6) have the most similarly structured advertisement calls. The main difference between the calls of the two species is in carrier frequency which may be accounted for by the difference in sizes of the two taxa (Table 5, Fig. 10). The similarities in call structure are consistent with the postulated close relationship of the two taxa suggested by Main (1957), and subsequently supported by the multivariate numerical analyses of morphology and features of life history carried out by Blake (1973)

and Thompson (1981). Although consistent in showing a close association between them, molecular studies do not help in resolving the relationships of *C. glauerti* and *C. signifera*. The albumin immunological analysis of Daugherty and Maxson (1982) places *C. signifera* closest to *C. riparia* (15 ID units), followed by *C. glauerti* and *C. paucisignifera* (both 24 ID units) and *C. georgiana* (29 ID units). The cladistic analysis of allozymes carried out by Barendse (1984) offers several interpretations and appears inconclusive about the relationships: in one scenario *C. glauerti* and *C. signifera* are grouped with *C. georgiana*. Barendse (1984) did not include *C. riparia* in his study. Roberts & Watson (1993) have reviewed the recent literature on relationships within some groups of Australian frogs.

Three of the species of *Crinia* described since the work of Main (1957) - *C. bilingua* Martin, Tyler & Davies (Martin *et al.* 1980), *C. remota* Tyler & Parker (Tyler & Parker 1974) and *C. riparia* Littlejohn & Martin (Littlejohn & Martin 1965) - have clearly pulsatile advertisement calls. Tyler & Parker (1974) noted the similarity of the advertisement calls of *C. remota* and *C. glauerti*, but they did not provide information about the recording temperatures. As the recording of the call of *C. remota* was obtained at Morehead, Papua New Guinea in January, the ambient temperatures presumably were much higher than those applying to recordings analysed in the present study. Hence, a direct comparison cannot be made with the calls of *C. glauerti* obtained at temperatures of 13.1 °C and lower. Blake (1973) noted that *Crinia riparia* lacks a tympanum and columella and placed the taxon into a different species group along with *C. tasmaniensis* (Günther). Because of the lack of a distinct tympanum in *C. remota* (Tyler & Parker 1974), it is suggested that there may not be a close relationship between this species and *C. glauerti*.

As the name indicates, the advertisement call of *C. bilingua* is strongly biphasic (Martin *et al.* 1980). In this species, males commence a calling sequence with short calls (<545 ms) of high pulse rate (>76 p s<sup>-1</sup>), and then gradually change over to long calls (>580 ms) of low pulse rate (<54 p s<sup>-1</sup>). Again, the high recording temperatures (wet-bulb air = 23.4–26.6 °C) mean that it is not possible to make a proper comparison with the advertisement call of *C. glauerti*. Even so, the audiospectrogram of the short call appears to be similar to some of the variations in the squeelching calls of *C. glauerti*. Martin *et al.* (1980) considered the functional significance of the two distinct calls of *C. bilingua* and raised the possibility that the short calls of higher pulse rate are mating calls, and that the long calls of lower pulse rate are territorial calls, the converse of the situation

for pulse rate in *C. signifera*. The long call of *C. biligua* contains about twice as many pulses ( $>27$ ) as in the advertisement call of *C. glauerti* ( $<16$ ). If allowance is made for the difference in temperature (by using a  $Q_{10}$  of 2), the pulse rate of *C. biligua* at 11° C would be about 20 p s<sup>-1</sup> and could overlap the pulse rates in the advertisement calls of *C. glauerti*. *Crinia biligua* possesses a tympanum but possible close affinities with *C. glauerti* were not considered by Martin *et al.* (1980).

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